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A Hybrid *Phlebodium* (Polypodiaceae, Polypodiophyta) and Its Influence on the Circumscription of the Genus

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Abstract.—The fern genus *Phlebodium* is traditionally described as having a row of costal areoles lacking included veins, with the sori located in extra-costal areoles and each sorus served by two veinlets. The discovery of a hybrid between *Phlebodium pseudoaureum* and *Polypodium pleurosorum* raises questions about the limits of *Phlebodium* and necessitates a revised taxonomic circumscription of the genus.

Key Words.—ferns, hybrid, Mexico, *Phlebodium*

The fern genus *Phlebodium* has a Neotropical distribution and has been thought to comprise three species: *P. aureum* (L.) J. Sm., *P. decumanum* (Willd.) J. Sm., and *P. pseudoaureum* (Cav.) Lellinger [syn. *P. areolatum* (Humb. & Bonpl. ex Willd.) J. Sm.] (see e.g., Proctor, 1989; Nauman, 1993; Mickel and Smith, 2004). When first recognized at generic rank, *Phlebodium* (R. Br.) J. Sm., based on *Polypodium* sect. *Phlebodium* R. Br., was a superfluous name because it included sect. *Pleopeltis* Humb. & Bonpl. ex Willd., an older name that should have been adopted under current rules (see Smith, 1981). Article 52.3 (McNeill *et al.*, 2005; see also its Ex. 15) is applicable to this matter. Since *Phlebodium* is based on a name-bringing synonym (in other words, it has a basionym, i.e., *Polypodium* sect. *Phlebodium* R. Br., that is legitimate), *Phlebodium* is not illegitimate. Because Smith's genus was a stat. nov., Art. 7.4 dictates that the type of R. Brown's section must also be the type of *Phlebodium*. Art. 10.2 establishes that the type must be either *P. aureum* or *P. decumanum*, given that these were the only two species included in sect. *Phlebodium* by Brown. *Phlebodium* was lectotypified by *Phlebodium aureum* (L.) J. Sm. (Smith, 1875), and this choice has been reaffirmed by several authorities (e.g., Copeland, 1947; Tryon and Tryon, 1982).

Phlebodium has usually been characterized by venation that is highly reticulate (but free near margins), with 1 to 4 rows of fertile costal polygonal areoles and two or three rows of alternate marginal sterile areoles (without free included veinlets) (Fig. 1J). The costal areoles include one secondary areole that extends laterally from secondary vein to secondary vein, with two

included excurrent veinlets meeting at apices. The genus is further characterized by having pinnatifid to pinnatisect blades (Fig. 1G).

Often, *Phlebodium aureum* has been treated in a broad sense (e.g., by Tryon and Stolze, 1993), to include also *Ph. pseudoaureum* and segregates of that species. Tryon and Tryon (1982) placed *Phlebodium aureum* s.l. and *Polypodium lowei* C. Chr. [= *Po. pleurosorum*] in with a group of Mexican and Mesoamerican species related to *Polypodium plesiosorum* Kunze, *P. subpetiolatum* Hook., and several other species. The *Po. plesiosorum* group is now thought to be closely related to true *Polypodium* (type: *Po. vulgare* L.), and less closely related to *Phlebodium* (Schneider *et al.*, 2006; Tejero-Díez, 2005).

In 2002, the first author (JDTD) discovered in Chiapas, Mexico, a specimen (Fig. 1 A–C) that appears to be a hybrid between the most common species of *Phlebodium* in Mexico, *Ph. pseudoaureum* (Figs. 1G–J), and a simply pinnate species of *Polypodium*, *Po. pleurosorum* Kunze ex Mett. (Figs. 1D–F). The plant has blades that are pinnate proximally and pinnatifid distally, a mixture of sori each served by a single vein or by two veins, and differential development of secondary costal sterile areoles (Figs. 1A and C). Its sori have abundant sporangia and mostly malformed spores (Fig. 2H). Some authorities have considered *Phlebodium* and *Polypodium* as only distantly related (e.g., Copeland, 1947, who thought *Phlebodium* to be derived from *Pleopeltis*), while others have thought them to be more intimately related (e.g., Tryon and Tryon, 1982, p. 691). Closer examination was made to see if *Polypodium pleurosorum* might in fact belong to *Phlebodium*. Moore (1855), in his description of *Polypodium pleurosorum* (under the name *Phlebodium inaequale* T. Moore) wrote: "The sori are large, round, situated in a single series near the midrib; sometimes seated on the apex of a veinlet within a costal areole, which is characteristic of *Goniophlebium*; sometimes on a veinlet exterior to the costal areole, sometimes at the point where two or more veins unite, which is the normal condition of *Phlebodium*. It is consequently an osculating species between the genus *Goniophlebium* and *Phlebodium*." He also noted that it resembles *Phlebodium aureum* but has truly pinnate fronds. Examination of herbarium specimens of *Polypodium pleurosorum* shows that although most of the sori are located in costal areoles and served by a single vein, there are occasional sori, especially distally, that are served by two veins.

Recent phylogenetic studies based on DNA molecular characters (Schneider *et al.*, 2004; Schuettpelz and Pryer, 2007) show that *Phlebodium pseudoaureum* and *P. decumanum* are sister to a clade comprising species of *Pecluma*. Sampled are *Pe. alfredii* (Rosenst.) M. G. Price, *Pe. eurybasis* (C. Chr.) M. G. Price, and *Pe. ptilodon* (Kunze) M. G. Price and two Mexican/Mesoamerican species of *Polypodium*, *Po. hartwegianum* Hook. and *Po. longepinnulatum* E. Fourn. the last two species, as well as some others, are probably better referred to *Pecluma*, but these transfers await more comprehensive sampling in the *Pecluma* clade. The *Phlebodium* + *Pecluma* clade is in turn sister to a large group (75+ spp.) of scaly polypods, the *Pleopeltis* clade (Otto *et al.*, in press), including scaly species usually included in *Polypodium* s.l. The true *Polypodium* clade, comprising *Po. vulgare* L. and allies (Haufler and Ranker,

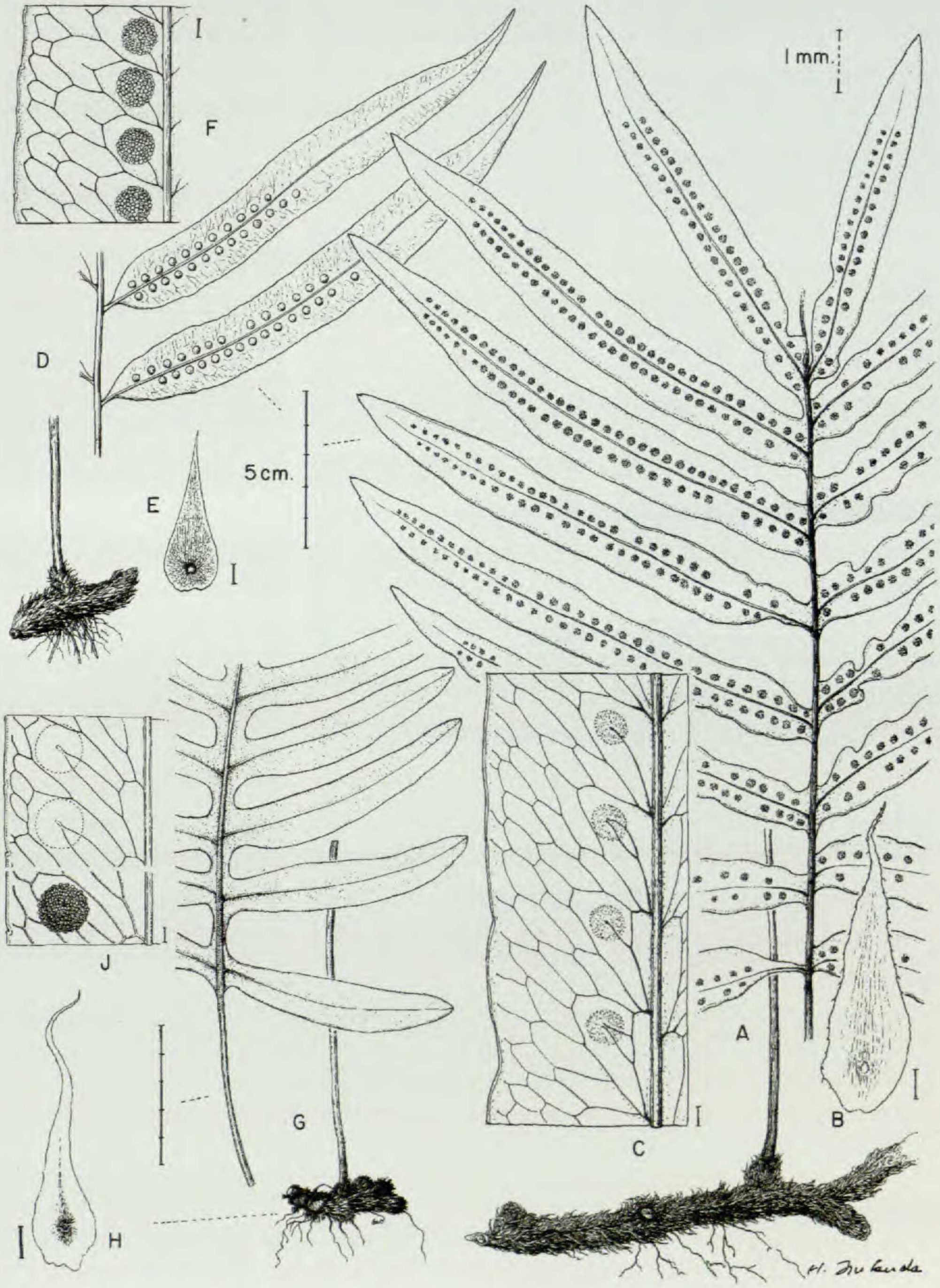

FIG. 1. A–C. *Phlebodium ×hemipinnatum* (*Tejero-Díez 4362*, NY). A. Habit. B. Rhizome scale. C. Pinna detail. D–F. *Phlebodium inaequale* (*Mickel 1099*, NY). D. Rhizome and pinnae. E. Rhizome scale. F. Pinna detail. G–J. *Phlebodium pseudoaureum* (*King & Soderstrom 4757*, MICH). G. Rhizome and blade. H. Rhizome scale. J. Pinna detail.

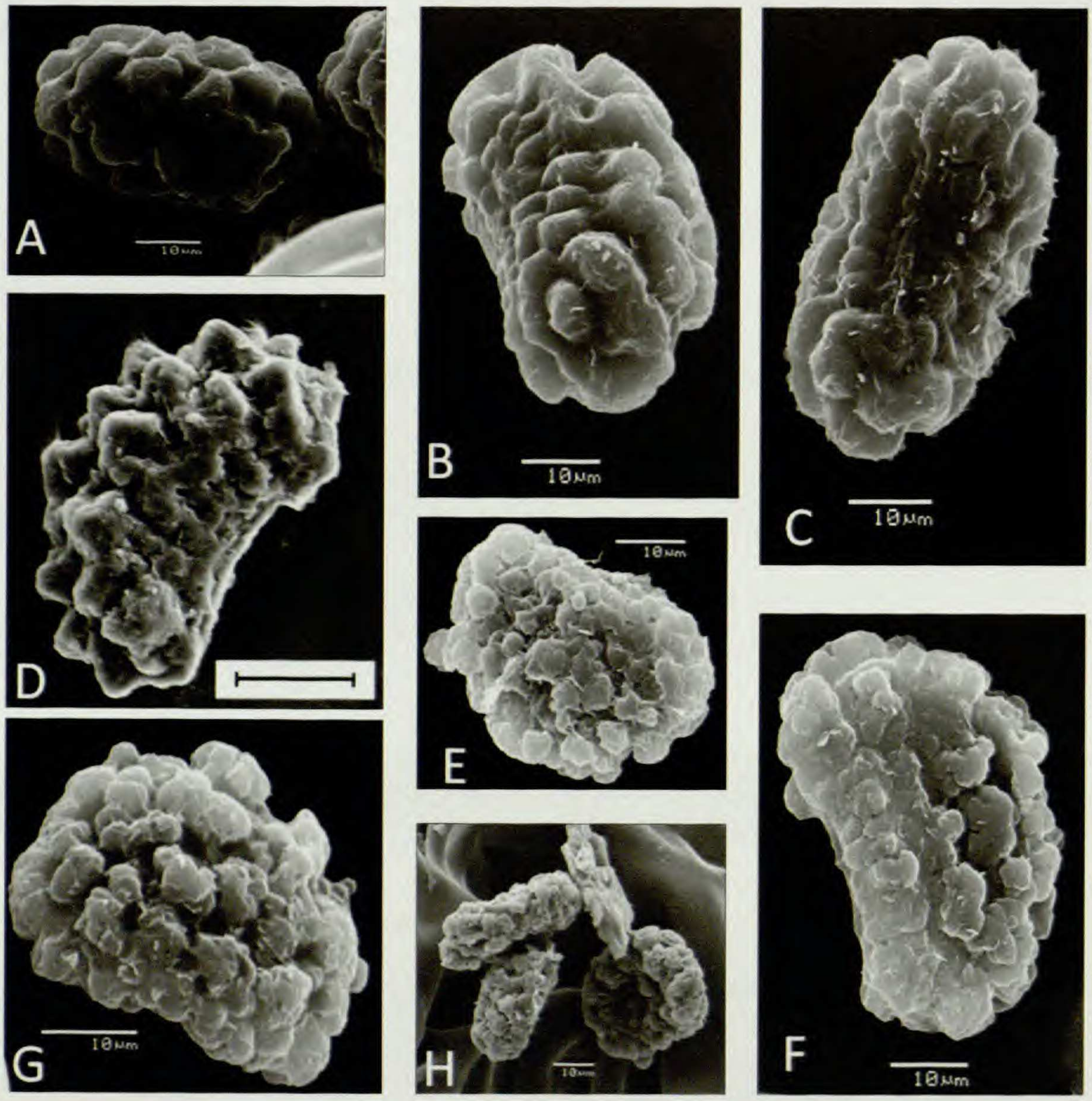

FIG. 2. Spores of *Phlebodium*. A–C. *Phlebodium inaequale* (*Tejero-Díez 4931*, IZTA). A. Distal view. B. Medial view. C. Proximal view. D. *Phlebodium pseudoaureum* (*Tejero-Díez 4195*, IZTA). Medial view (bar 20 µm). E–H. *Phlebodium* ×*hemipinnatum* (*Tejero-Díez 4362*, MEXU). E. Medial view. F, G. Proximo-medial view. H. Malformed spores.

1995), is yet more distantly related to *Phlebodium*. *Phlebodium inaequale* has now also been sampled for DNA (Schneider, unpubl. data), and nucleotide sequence data show that *Phlebodium*, as redefined here and including the newly transferred *P. inaequale*, is monophyletic, with strong bootstrap and Bayesian support, sister to the *Pecluma* alliance (Schneider, pers. comm.)

Proctor (1989) reported that in Puerto Rico, where *Phlebodium aureum*, *Ph. pseudoaureum*, and *Ph. decumanum* occur together, both *P. pseudoaureum* and *P. decumanum* appear to be diploid, *Phlebodium aureum* s.s. is their fertile, allotetraploid hybrid, and at least one sterile, triploid backcross hybrid was reported. Chromosome counts for *Phlebodium* include three counts of $2n = 74$ (diploid, based on $x = 37$) for *Ph. decumanum* from Trinidad (Walker,

1985), three counts of $n = 74$, $2n = 147$ for *Ph. aureum* from Trinidad and Tobago (Walker, 1985), and four counts $n = 37$, 2n = 74 of *Ph. aureum* s.l. from Jamaica and Mexico (Walker, 1966; Mickel and Smith, 1977, reported as *Po. araneosum* M. Martens & Galeotti, now considered a synonym of *Ph. pseudoaureum*). These last diploid counts likely pertain to the species now called *Ph. pseudoaureum*, and not the true *Ph. aureum*, which appears to be tetraploid. Walker (1985) reported spontaneous, sterile, triploid hybrids between what he called *Po. aureum* s.l. and *Po. decumanum* in Trinidad. There is also an early report of a hybrid called *Phlebodium* ×*schneideri*, reputed to be the hybrid between *Po. aureum* s.l. and *Po. vulgare* L. (Schneider, 1894). The parentage of this hybrid now seems in doubt, because of the relatively distant relationship between *Phlebodium* and *Polypodium*, as currently defined.

In an attempt to verify hypothesized relationships among species of *Phlebodium*, Caruso (1985) studied living plants of *Phlebodium aureum*, *Ph. pseudoaureum*, and *Ph. decumanum* growing in the greenhouses of the New York Botanical Garden. Although cytological studies were unsuccessful, measurements of spores and stomatal guard cells showed significant differences, with the tetraploid, *Ph. aureum* having the larger measurements.

The rarity of the Tejero-Díez collection (*4362*) and its morphological intermediacy suggest that it is a hybrid, and with its significant bearing on the circumscription of the genus *Phlebodium*, we hereby give it a hybrid name.

Phlebodium ×***hemipinnatum*** Tejero, Mickel and A. R. Smith, **hyb. nov.** TYPE.—MEXICO: **Chiapas**, Mpio. San Cristóbal de las Casas, Km 67 de la carretera federal 190, Tuxtla Gutiérrez a San Cristóbal de las Casas (16° 42′ 23″ N, 92° 46′ W), bosque de *Pinus-Quercus*, 2440 m, 6 Ago 2002, *Tejero-Díez 4362* (Holotype: MEXU; isotypes: IEB, IZTA, NY, UAMIZ). **Figs. 1A–C.**

Phlebodio pseudoaureo atque *Polypodio pleurosoro* proxima, sed laminis hemipinnatis, id est basis pinnatis apiceque pinnatifidis, plane differt.

Rhizomes long-creeping, 4–6 mm diam. (excluding scales), pruinose, densely scaly; *rhizome scales* 8–12 × 2–4 mm, ovate, long-attenuate, yellowish brown, each with enlarged, round, peltate base, darker at point of attachment, margins denticulate to short-ciliate and erose throughout, with short to long, flexuous, contorted, hairlike tips; *fronds* (55) 60–70 cm long; *stipes* 1/3–1/2 the frond length, brown, glabrous; *blades* ovate-deltate to broadly-oblong, 26–35 cm wide, 1-pinnate at middle basal part, becoming pinnatifid above the middle, terminal segment subconform, 5–16 cm long; pinnae (segments) 8–12 pairs, 12–30 mm wide, linear-oblong to linear-lanceolate, some falcate, acuminate, glabrous, green-yellowish, margins entire to repand; *veins* netted, free near margins, with 1 row of fertile costal polygonal areoles, each with a single simple or bifurcate, excurrent included veinlet or 2 veinlets that form a secondary areole and meet at their tips, 2–3 rows of similar areoles closer to pinna margins, these mostly without included veinlets; *sori* round, 2–3 mm diam., submedial, one row on each side of the costa; *spores* mostly malformed,

bilateral, monolete, (33)39(45) × (22)26(33) μm, tuberculate, tubercles dome-shaped, somewhat overlapping, amber.

PARATYPE.—MEXICO: **Chiapas**, Mpio. Tenejapa, a 3.5 km al NE del paraje Balum Canal (16° 48′ 05″ N, 92° 31′ 50″ W), Acahual derivado de bosque de *Pinus-Quercus*, 2200 m, 8 Mar 1995, *Ramírez-Marcial & Hernández-Rojas 654* (MEXU!, ECOSUR - herbarium of the Colegio de la Frontera Sur, Chetmul, Quintana Roo, Mexico).

HABITAT.—Epiphytic in pine-oak forests and adjacent disturbed areas; 2200–2500 m.

DISTRIBUTION.—Mexico, Chiapas, montane areas.

The existence of this new hybrid, with characters intermediate between *Phlebodium pseudoaureum* and *Polypodium pleurosorum*, causes us to conclude that the latter species can once again be included in the genus *Phlebodium*, with the earliest available name, *Ph. inaequale* T. Moore. Impetus for the recircumscription of polypod genera has been given by several other recent phylogenetic studies on Polypodiaceae, most importantly the one by Schneider *et al.* (2004), outlining a global phylogeny for the family. Subsequently, several other papers directed toward the placement of problematic Neotropical polypods have appeared (e.g., Krier *et al.*, 2007; Schneider *et al.*, 2006; Tejero-Díez, 2005), are in press (Krier *et al.*, 2008), or have been submitted for publication (Otto *et al.*, in press). The redefinition of *Phlebodium* also recalls the recent recircumscription of the polypod genus *Microgramma*, necessitated by the finding of a new and radically different species of the genus in coastal Brazil (Salino *et al.*, in press).

Cladistic analysis of morphological characters in species of *Polypodium* and related taxa (Tejero-Díez, 2005) suggests that the critical characters separating *Phlebodium* from its sister group (*Pecluma*, and Mexican/Mesoamerican species allied to *Pecluma* but still placed in *Polypodium*; Schneider *et al.*, 2004; Schuettpelz and Pryer, 2007) are: a) spores with tuberculate ornamentation (Fig. 2A–H; b) small size of spore body (33) 38 (45) μm; and c) the presence of several rows of marginal sterile polygonal areoles.

Of the aforementioned characters, the spore ornamentation in *Phlebodium* and the smaller spore size are unique in Polypodiaceae, but the ornamentation is somewhat similar to spores of *Polypodium arcanum* Maxon and some species of *Serpocaulon* (Tryon and Lugardon, 1991; Tejero-Díez, 2005). It is clear that the taxonomic limits of *Phlebodium* cannot be governed by the way in which the internal veinlets of the main costal areoles are organized.

The species of *Phlebodium* and the newly described hybrid can be separated by the following key:

1. Blades 1-pinnate, at least proximally; sori each at the end of a simple or bifurcate veinlet; secondary costal areoles absent or irregularly so.
   2. Blades pinnate throughout their length. . . . . *P. inaequale*
   2. Blades pinnate proximally but pinnatisect or pinnatifid distally. . . . . *P. ×hemipinnatum*
1. Blades pinnatifid or pinnatisect; sori each at the end of two veinlets; secondary costal areoles regularly present.

3. Sori in 1 row on each side of costae; (170–)550–2500 m. . . . . *P. pseudoaureum*
3. Sori in 2 or more rows on each side of costae; 0–500 m.
   4. Sori on 3 or more rows on each side of costae. . . . . *P. decumanum*
   4. Sori on 2 (infrequently 1) rows on each side of costae.. . . . . .*P. aureum*

The use of the name *Phlebodium inaequale* T. Moore for what has been called *Polypodium pleurosorum* Kunze ex Mett. requires a brief explanation. The former name was published first by Moore (1855), but when treated as belonging in *Polypodium* cannot be used because of the existence of an earlier homonym, *Polypodium inaequale* Link, published in 1833 (Mickel and Smith, 2004).

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